

Evolution of human music through sexual selection

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Introduction: A Darwinian approach to music evolution

“... it appears probable that the progenitors of man, either the males or females or both sexes, before acquiring the power of expressing their mutual love in articulate language, endeavoured to charm each other with musical notes and rhythm.” (Darwin, 1871, pp. 880)

In *The descent of man, and Selection in relation to sex*, Darwin (1871) devoted ten pages to bird song and six pages to human music, viewing both as outcomes of an evolutionary process called sexual selection. Darwin's idea that most bird song functions as a courtship display to attract sexual mates has been fully supported by biological research (e.g. Catchpole & Slater, 1995), but his idea that human music evolved to serve the same function have been strangely neglected. Although there has been much written about the origins of human music (e.g. Blacking, 1987; Dissanayake, 1988, 1992; Knight, 1991; Rousseau, 1966; Storr, 1992; Tiger, 1992), very few theorists have taken a serious adaptationist approach to the question. Those who have, have usually searched in vain for music's survival benefits for the individual or the group, overlooking Darwin's compelling argument that music's benefits were primarily reproductive, and best explained by the same sexual selection processes that shaped bird song. This chapter has the simple goal of reviving Darwin's original suggestions that human music must be studied as a biological adaptation, and that music was shaped by sexual selection to function mostly as a courtship display to attract sexual partners. Fortunately, after a century of obscurity, Darwin's theory of sexual selection itself has already undergone a renaissance in biology over the last two decades, so biology offers many new insights about courtship adaptations, which will be applied here to human music.

The historical analogy between the study of bird song and the study of human music may prove instructive. Before Darwin, the natural theologians such as William Paley considered bird song to have no possible function for the animals themselves, but rather to signal the creator's benevolence to human worshippers through miracles of beauty. Bird song was put in the category of the natural sublime, along with flowers, sunsets, and alpine peaks, as phenomena with an aesthetic impact too deep to carry anything less than a transcendental message. The idea that bird song would be of any use to birds was quite alien before about 1800. With the rise of natural history, writers such as Daines Barrington in 1773 and Gilbert White in 1825 (cited in Darwin, 1871) argued that bird song must have some function for the animals that use it, but must arise exclusively from male rivalry and territorial competition. They recognized that male birds sing much more than females, and sing mostly in breeding season. But they insisted that song was a form of vocal intimidation between males rather than attraction between the sexes.

Darwin agreed that some songs function to intimidate, but argued that female choice for male singing ability was the principal factor in the evolution of bird song: “The true song, however, of most birds and various strange cries are chiefly uttered during the breeding-season, and serve as a charm, or merely as a call-note, to the other sex” (Darwin, 1871, p. 705). Against the hypothesis that bird song somehow aids survival, Darwin cited observations that male birds sometimes drop dead from exhaustion while singing during the breeding season. His sexual selection theory was perfectly concordant with the idea that males sacrifice their very lives in the pursuit of mates, so that their attractive traits live on in their offspring.

The history of theorizing about the evolution of human music shows many of the same themes. Many commentators have taken Paley’s creationist, transcendental position, claiming that music’s aesthetic and emotional power exceed what would be required for any conceivable biological function. Claude Levi-Strauss (1970, p. 18), for example, took a position typical of cultural anthropology in writing “Since music is the only language with the contradictory attributes of being at once intelligible and untranslatable, the musical creator is a being comparable to the gods, and music itself the supreme mystery of the science of man.” Where such commentators have recognized any need for consistency with evolutionary principles, they usually explain music as side-effect of having a big brain, being conscious, or learning culture. As we shall see, none of these explanations are adequate if music can be shown to be a legitimate adaptation in its own right. Other theorists have adopted the pre-Darwinian natural historians’ rather narrow view of biological function as centered on competition for survival. This has led to desperate searches for music’s contribution to pragmatic survival problems in Pleistocene Africa, our ancestral environment. Here, quandaries arise. No one has ever proposed a reasonable survival benefit to individuals taking the time and energy to produce music, which has no utility in finding food, avoiding predators, or overcoming parasites. But if one falls back on claiming survival benefits to the group, through some musical mechanism of group-bonding, then one ends up in the embarrassing position of invoking group selection, which has never been needed to explain any other trait in any mammalian species (see Williams, 1966). If evolution did operate according to survival of the fittest, human music would be inexplicable.

Consider Jimi Hendrix, for example. This rock guitarist extraordinaire died at the age of 27 in 1970, overdosing on the drugs he used to fire his musical imagination. His music output, three studio albums and hundreds of live concerts, did him no survival favours. But he did have sexual liaisons with hundreds of groupies, maintained parallel long-term relationships with at least two women, and fathered at least three children in the U.S., Germany, and Sweden. Under ancestral conditions before birth control, he would have fathered many more. Hendrix’s genes for musical talent probably doubled their frequency in a single generation, through the power of attracting opposite-sex admirers. As Darwin realized, music’s aesthetic and emotional power, far from indicating a transcendental origin, point to a sexual-selection origin, where too much is never enough. Our ancestral hominid-Hendrixes could never say, “OK, our music’s good enough, we can stop now”, because they were competing with all the hominid-Eric-Claptons, hominid-Jerry-Garcias, and hominid-John-Lennons. The aesthetic and emotional power of music is exactly what we would expect from sexual selection’s arms race to impress minds like ours.

Darwin on human music

Though Darwin devoted only a few pages of *The descent of man* to the role of sexual selection in the evolution of human music (Darwin, 1871, pp. 875-881), his insights remain so apposite that they are worth reviewing here. Darwin seems to have considered music the single best example of mate choice having shaped a human behavioral trait. He first sets the context by reminding the reader that sounds generally evolve for reproductive functions: "Although the sounds emitted by animals of all kinds serve many purposes, a strong case can be made out, that the vocal organs were primarily used and perfected in relation to the propagation of the species" (Darwin, 1871, p. 875). He reviews as examples the sounds of frogs, toads, tortoises alligators, birds, mice, and gibbons, which are produced only in the breeding season, usually only by males, but sometimes by both sexes. He then reviews the anatomy of sound perception to argue that the capacity to perceive musical notes could easily have begun as a side-effect of the capacity to distinguish noises in general: "an ear capable of discriminating noises -- and the high importance of this power to all animals is admitted by every one -- must be sensitive to musical notes" (Darwin, 1871, p. 877). The famous 1868 paper by Helmholtz on acoustic physiology is cited to explain why many animals would converge on using tones that belong to human musical scales. Darwin concludes with a strong critique of the natural theology position, arguing that if male birds sing to females, it must be because female birds are impressed by singing: "unless females were able to appreciate such sounds and were excited or charmed by them, the persevering efforts of the males, and the complex structures often possessed by them alone, would be useless; and this is impossible to believe" (Darwin, 1871, p. 878).

Immediately after rejecting the possibility that animal sounds are useless, Darwin ponders the apparent frivolity of human music: "As neither the enjoyment nor the capacity of producing musical notes are faculties of the least use to man in reference to his daily habits of life, they must be ranked among the most mysterious with which he is endowed" (Darwin, 1871, p. 878). He then cites the ubiquity of music across cultures, and even mentions some recently unearthed Palaeolithic flutes made from reindeer bone to illustrate music's antiquity. He goes on to mention how music capacities may emerge spontaneously and reliably in human development: "We see that the musical faculties, which are not wholly deficient in any race, are capable of prompt and high development" (Darwin, 1871, p. 878). He then illustrates how music arouses strong emotions, and how love is the most common lyrical theme in songs. Apart from his rather patronizing Victorian attitude towards non-European music, Darwin's strategy for arguing that human music is a biological adaptation and a product of sexual selection is almost identical to that which a modern evolutionary psychologist would use. Darwin summarizes: "All these facts with respect to music and impassioned speech become intelligible to a certain extent, if we may assume that musical tones and rhythm were used by our half-human ancestors, during the season of courtship (Darwin, 1871, p. 880). As the coup de grace, he pre-empts the objection that musicians don't mean anything sexual when they perform, by reminding us that a biological function requires no conscious awareness: "The impassioned orator, bard, or musician, when with his varied tones and cadences he excites the strongest emotions in his hearers, little suspects that he uses the same means by which his half-human ancestors long ago aroused each other's ardent passions, during their courtship and rivalry" (Darwin, 1871, p. 881).

Darwin was not troubled by the fact that both men and women produce music. He admits that the capacity and love for singing and music are not a "sexual character" in the sense of a sexually dimorphic trait (Darwin, 1871, p. 875). In the three hundred

pages on sexual selection preceding his analysis of human music, Darwin noted many sexually-selected traits present in both sexes. His remarks on prehistoric marriage, and on sexually-selected physical traits present in both sexes, suggest that he assumed both male and female mate choice among our ancestors.

What can we add to Darwin's hypothesis that human music arose through mate choice? Well, we know more about music now, and we know more about mate choice, and we know more about mental adaptations. Although Darwin laid the foundations, a modern Darwinian approach to music can draw on the full power of evolutionary biology, evolutionary psychology, and evolutionary anthropology.

An adaptationist approach to music

Before getting too deeply into the relevance of sexual selection theory to music, it is important to step back and ask about the relevance of evolutionary theory in general. There are many ways of asking about the origins of music. But evolutionary biologists would focus on four key questions of increasing specificity (see Williams 1966; Tooby & Cosmides, 1990, 1992). First, what is "music" for? Second, what adaptive functions are served by the specific behaviours of singing, chanting, humming, whistling, dancing, drumming, and instrument-playing? Third, why did the fitness benefits of music-making and music-listening exceed the fitness costs? Fourth, consider music as a set of signals emitted to influence the behaviour of other organisms (see Dawkins & Krebs, 1978): Who generates these signals, under what conditions, to what purpose? And who receives these signals, with what sensitivity, resulting in what behavioural changes, benefiting whom?

All of these questions put music in the adaptationist arena, where theories have to play by very strict rules. In this arena, it is not so important to worry about how to define music, exactly when it evolved, or what sequence of modifications occurred to transform non-musical apes into musical humans. Most of the speculation about the "origins" of music identifies some ape or human behavior that shares certain features with music, such as the prosody seen in mother-infant ritualized verbal exchanges (Dissanayake, this volume; Storr, 1992), or adult speech (Pole, 1924), and then supposes that the identification of a plausible origin is sufficient to explain a complete adaptation. Evolution just doesn't work like that. Instead of speculating about precursors, the adaptationist approach puts music in a functional, cost-benefit framework and asks theories for just one thing: *show me the fitness!*

The fitness means the survival or reproductive advantages of a trait that out-weigh its biological costs. Every trait, whether bodily or behavioural, has costs, because they all require matter and energy that might be better spent on something else. Music production and dancing would have had particularly high costs for our ancestors: they're noisy so they could attract predators and hostile competitors, they require energetic body movements sustained for hours, they require long periods of practice to perform well, and they keep your sleepy babies from getting their rest. Almost all traits that could evolve in a particular species don't evolve, because their fitness benefits do not exceed their fitness costs. Only a tiny minority do. To explain why music evolves in our lineage means explaining why it conferred net fitness benefits on our ancestors.

Of course, not all things that a species does require an adaptationist explanation of this sort. Only adaptations do. The first question for biomusicologists must be: is human

music a legitimate, complex, biological adaptation? If it isn't, then it might be explicable as a side-effect of other evolutionary or cultural processes. But if it is, then the rules change: complex adaptations can only evolve through natural selection or sexual selection (Williams, 1966; Dawkins, 1995). That's it. There are no other options, and if any musicologist is lucky enough to discover some other way of explaining adaptive complexity in nature, they can look forward to a Nobel prize in biology.

Both natural selection and sexual selection boil down to one principle: some genes replicate themselves better than others. Some do it by helping their bodies survive better, and some by helping themselves to reproduce better. While individuals are the units of survival, genes are the units of selection and replication, and selection views the individuals as transient vehicles for passing on their genes (Dawkins, 1976, 1995). Between the level of genes and the level of individuals, there is the level of adaptations, which are units of biological function. Most complex adaptations grow through the interaction of many genes, which were selected gradually over many generations. Because the chance combination of genes necessary to produce a complex adaptation are astronomically unlikely in a single generation, cumulative selection over many generations is the only known mechanism for producing such adaptations (Dawkins, 1995). This view of genes as the units of selection and adaptations as the unit of function is sometimes called "adaptationism" or "neo-Darwinism" or "selfish gene theory", but it has become the dominant, mainstream framework for modern biology, including animal behavior studies, physical anthropology, and evolutionary psychology. If we want ideas about the origins of music to be taken seriously by these communities, we have to play by their adaptationist rules, which have proven so successful for explaining so many other apparently baffling biological phenomena.

Music, like language (Pinker, 1994), fulfils many of the classic criteria for being a complex biological adaptation in our species. It is universal across cultures and universal across all epochs of recorded history. It unfolds according to a standard developmental schedule, resulting in high musical capacity in all normal human adults relative to the musical capacities of closely related species: almost everyone can learn a melody, carry a tune, and appreciate musical performances by others. Music seems to involve specialized memory capacity such that normal adults can almost instantly recognize and reproduce any of thousands of learned melodies. Musical capacities show strong cortical lateralization and are localized in standard, special-purpose cortical areas. Human music has clear analogs in the acoustic signals of other species (such as bird song, gibbon song, and whale song), suggesting convergent evolution. Music can provoke very strong emotions, suggesting not only biological adaptations for production, but also for reception. With respect to these nine adaptationist criteria, music differs clearly from other human abilities such as proving mathematical theorems, writing legal contracts, or piloting helicopters, which depend on a tiny minority of individuals being able to acquire counter-intuitive skills through years of difficult training. Some ethnomusicologists such as John Blacking (1976, p. 7) have also recognized that music is an adaptation: "There is so much music in the world that it is reasonable to suppose that music, like language and possibly religion, is a species-typical trait of man. Essential physiological and cognitive processes that generate musical composition and performance, may even be genetically inherited, and therefore present in almost every human being."

The adaptationist framework has recently been extended to cope with animal signalling systems (Dawkins & Krebs, 1978; Hauser, 1996; Krebs & Dawkins, 1984), which would

include human music. It seems strange at first for an animal to produce a costly signal that does not directly influence its environment. A signal that simply “expressed feelings” without having any fitness payoffs would never evolve. Even a signal that “communicated information” would never evolve unless an animal gained some indirect survival or reproductive benefit to that information having been sent to another animal. Altruistic information-broadcasting has no place in nature: there are no species evolved to play the role of the BBC World Service. Because such indirect benefits of signalling are relatively rare, true animal “communication” is rare. The major exception is signalling between close relatives that share many of the same genes.

Most animal signal systems have been successfully analyzed as adaptations that manipulate the signal receiver’s behavior to the signaller’s benefit. Signals are usually selfish. If we take an adaptationist approach to music, and if music is not just directed at kin, then we must analyze music as a biological signal that manipulates receivers to the benefit of signallers. Many such manipulative signals are sent between species: bee orchids attract male bees by looking and smelling like female bees (Darwin, 1862); warning coloration keeps unpalatable insects from being eaten by their predators (Wallace, 1889). A few manipulative signals, such as music, are sent primarily within a species, from one conspecific to another. Such conspecific signals tend to fall into a very small number of categories (Hauser, 1996). There are threats exchanged between competitors, warning calls exchanged between kin (to signal the proximity of a dangerous predator), contact calls exchanged between group members (to keep the group together during movement), dominance and submission signals, and courtship displays. Of these, courtship displays are almost always much more complex, more varied, more prolonged, more energetically expensive, and more interesting to human observers. By these criteria, if an alien biologist were asked for their best guess about the evolutionary function of human music as a conspecific signal, they would almost certainly answer: music is a sexually selected courtship display, like almost all other complex, varied, interesting sounds produced by other terrestrial animals.

Music as a courtship adaptation does not mean that music stems from a Freudian sublimated sex drive. Sexually-selected adaptations do not need to feel very sexy to their users. A trait shaped by sexual selection does not have to include a little copy of its function inside, in the form of a conscious or subconscious sexual motivation (see Tooby & Cosmides, 1990, 1992). The male human beard, although almost certainly an outcome of sexual selection through female mate choice, is not a jungle of hidden, illicit motives. It simply grows, and displays that its possessor is a sexually mature male, without having any idea why it’s doing that. Even psychological adaptations like music production may work similarly, firing off at the appropriate age and under the right social circumstances, without their possessor having any idea why they suddenly feel “inspired” to learn the guitar and play it where single people congregate.

Identifying an adaptation and its function does not require telling the phylogenetic story of how the adaptation first arose at a particular time and place in prehistory, and how it underwent structural transformation through a series of intermediate stages. Even for morphological adaptations, biologists often have no idea when the adaptations that they study first arose, or exactly how they reached their current form. For most psychological adaptations that leave no fossil record, it is not even possible to reconstruct phylogeny in this sense. Nor is it necessary. Adaptationist analysis does not worry very much about origins, precursors, or stages of evolutionary development; it worries much more about the current design features of a biological trait, its fitness costs and benefits, and its

manifest biological function. This is good news for theories of music evolution. It is just not very important whether music evolved two hundred thousand years ago or two million years ago, or whether language evolved as a precursor to music. The adaptationist's job is to look at the adaptation as it is now, to document its features and distribution within and across species, and to test hypotheses concerning its biological function against this evidence.

In sum, music is a complex adaptation, and it has costs, but no identifiable survival benefits. Therefore, it is most likely to have evolved due to its reproductive benefits. Because there are such clear functional analogs between human music and bird song, gibbon song, and whale song, which all seem to have been shaped by Darwin's process of sexual selection through mate choice, music seems most likely an outcome of mate choice. The principal biological function of music, then, is sexual courtship.

Design features of music as a sexually-selected adaptation

Before opening the toolbox of sexual selection theory any further, we should pause, summarize, and sharpen the preceding arguments. Music, like art, language, and ideology, shows the hallmarks of being a complex behavioral adaptation. It is easy and fun to learn for humans but very hard for artificial intelligence programs (suggesting that its production is objectively very complex and difficult, though seemingly effortless). It is universal across cultures and across history. It is universal across normal individuals, though with some genetic heritability in aptitude. It develops spontaneously according to a standard life-history pattern, without formal instruction or conscious awareness of its underlying principles (except for professional musicians). But music also has special features as products of sexual selection. It is spontaneously practiced and produced despite their energetic costs and lack of survival utility. Over the short term, it is used conspicuously in courtship, and its production tends to decline after mating (as Miles Davis famously observed, male musicians, like athletes, avoid having sex before important concerts, because they need the sexual "edge" to play well). Over the life span, public music production rockets upwards after puberty, reaches its peak in young adulthood during the period of most intense courtship, and declines gradually with age and parenting demands. Musical tastes lead to strong assortative mating. Finally, music is functionally analogous to sexually-selected acoustic displays in other species.

Sexual selection theory: The basics

Darwin (1871) identified two different kinds of sexual selection: aggressive rivalry, and mate choice. Rivalry, especially between males, tends to produce weapons, such as sharp teeth, large horns, and strong muscles. Mate choice, especially by females, tends to produce ornaments, such as colorful tails, innovative sounds, and musky smells. Although Darwin provided overwhelming evidence for the importance of female mate choice in producing male ornaments, biologists after Darwin focused almost exclusively on male rivalry, rejecting the possibility of female choice (Cronin, 1991). For a century, sexual selection was seen as a process where active, competitive males struggled for "possession" of passive females, by acquiring territories and status, and repelling rivals. Ornaments were usually interpreted as species-recognition signals, for helping animals avoid mating with the wrong species. Only in the last couple of decades has the picture changed, with an astounding vindication of Darwin's mate choice idea in hundreds of experimental and theoretical studies (Andersson, 1994; Ridley, 1993). Research on sexual selection through mate choice is currently one of the most active areas of

behavioral science, with papers saturating all the major animal behavior journals. The sophistication and complexity of mate choice theory has grown enormously in recent years. But for our purposes, we only need to understand two key ideas: mate choice for indicators, and mate choice for aesthetic displays.

Music as a set of sexually-selected indicators

The idea of indicators is that sexual selection shapes animals to advertise reproductively important things like age, health, fertility, status, and general fitness (see Andersson, 1994). For example, the peacock's tail may function as an indicator, because unhealthy, weak, peacocks cannot grow very large tails, and even if they could, they could not escape from the predators that easily notice large tails. The result is that the size of a peacock's tail statistically correlates with the peacock's age, health, and heritable fitness. Peahens thus have a strong incentive for paying attention to tail size, because by mating with a large-tailed peacock, they are getting good genes that will give their offspring survival and reproductive advantages. While some indicators reveal good genes, others reveal good resources, good parenting skills, or good fertility.

Indicators are usually subject to the "handicap principle" (Zahavi, 1975, 1997) that they must have high costs in order to be reliable. Cheap, easy-to-grow, easy-to-maintain indicators could be faked too easily by unhealthy, unfit individuals, so the indicator would lose its informative value. Technically, the key feature is that the indicator must have a higher relative cost to an unfit animal than it does to a highly fit animal (Grafen, 1990). For example, male elephant seals typically get to breed only by becoming the single most dominant male on a beach full of hundreds of females, which requires constantly fighting off all the other males with hardly any sleep or food for weeks on end. Being dominant might cost a male many thousands of calories a day in food energy previously stored as fat. Thin males might have the strength to become dominant for short periods, but each day may burn off 10% of their fat reserves. They cannot long bear the calorie cost of chasing off all their rivals, and such males usually starve to death early in the breeding season. They are replaced by fatter males for whom the same calorie cost represents perhaps only 2% of their fat reserves per day, and for whom the relative, marginal cost of dominance is lower. Thus, dominance in male elephant seals is a reliable indicator of fat reserves, and hence of male foraging ability. Thus, the traits that are most informative as indicators are those that are very easy to mess up, that are highly sensitive to disruption by poor nutrition, injury, parasites, pathogens, genetic inbreeding, or developmental disorders. This leads to the apparent paradox that animals advertise their fitness with those displays that, being most costly, most reduce their fitness.

Many traits have been shown to function as reliable indicators in various animals (Andersson, 1994). Body size indicates age and nutritional state. Body symmetry indicates resistance to developmental insults such as disease and injury. Bright colors indicate ability to escape from predators, and resistance to parasites that dull those colors. Even more numerous are behavioral indicators. The loudness of songs indicates energy level in tungara frogs. The length of roaring displays indicates physiological endurance in red deer. The size of prey given as nuptial gifts by scorpionflies indicates foraging skill and strength. Territory quality in many birds indicates dominance and fighting ability. All of these evolved under sexual selection, favored by mate choice.

In large-brained animals, there are good reasons to suspect that complex psychological adaptations could function particularly well as sexually-selected indicators. Brains are very complex, hard to grow, and expensive to maintain. Higher cortical functions can be easily disrupted by poor nutrition, disease, injury, and low status (leading to depression). Moreover, in primates, probably half of all genes are involved in brain growth, and perhaps a third a uniquely expressed in brain growth. This means that for humans, with about 100,000 genes, brain-indicators could reveal the state of up to 50,000 genes in prospective mates. Thus, brain functioning provides a clear window onto the quality of a large proportion of an animal's heritable genome. The behaviors that large brains generate can function as a particularly sensitive indicator, and mate choice would be unlikely to ignore such a mine of useful information. Any behavioral signal that's difficult to produce if one is sick, injured, starving, old, depressed, or brain-damaged can function as a reliable indicator, so could become amplified by sexual selection into a courtship display.

This argument has an almost inescapable corollary: the more important brains became in human survival and reproduction, the more incentive mate choice would have had to focus on brain-specific indicators. Even if one supposed that hominid brains originally started to expand through natural selection for better tool-making or higher social intelligence (rather than directly under sexual selection), sexual selection would tend to hijack brain evolution. If natural selection favored tool-making ability, sexual selection would quickly come to favor exaggerated displays of the mental and physical skills relevant in tool-making. Likewise for almost any naturally-selected mental capacity: if individuals vary in the capacity in ways that can be perceived in mate choice, there are incentives for mate choice to pre-empt natural selection and filter out individuals with lower capacities.

Music, considered as a concrete behavior rather than an abstract facet of culture, shows many features that may function as indicators. Dancing reveals aerobic fitness, coordination, strength, and health. Because nervousness interferes with fine motor control, including voice control, singing in key may reveal self-confidence, status, and extroversion. Rhythm may reveal the brain's capacity for sequencing complex movements reliably, and the efficiency and flexibility of the brain's "central pattern generators". Likewise, virtuosic performance of instrumental music may reveal motor coordination, capacity for automating complex learned behaviors, and having the time to practice (which in turn indicates not having heavy parental responsibilities already, and hence sexual availability). Melodic creativity may reveal learning ability to master existing musical styles and social intelligence to go beyond them in producing optimally exciting novelty.

These indicator functions for music are all speculative, but there are well-established empirical methods in biology for testing indicator hypotheses. First, one can look for a population-level correlation between the indicator's value (e.g. dancing ability) and the putative underlying trait that it is supposed to indicate (e.g. aerobic capacity and motor coordination). Second, one can look for individual-level effects by experimentally manipulating the underlying trait and measuring its effect on the indicator (e.g. improve aerobic capacity through three months of exercise) and seeing if it improves the indicator value (e.g. dancing ability). Third, one can do experiments on mate preferences to see whether people are more sexually attracted by individuals with higher rather than lower indicator values, and to see whether they attribute higher underlying trait values to those with high indicator values. None of these empirical studies have yet been done, to my

knowledge, to analyze human music as a set of sexually-selected indicators. Many such studies would have such obvious outcomes that doing them hardly seems necessary. But such studies, even the obvious ones like showing that healthier peacocks have larger tails (Petrie et al., 1992), have been critical in demonstrating the importance of indicators in other species.

Music as a set of sexually-selected aesthetic displays

While indicators reveal useful information, aesthetic displays play upon psychological foibles. The basic idea of aesthetic displays is that mate choice works through animal sensation, perception, and cognition, and these psychological processes sometimes have biased sensitivities that other animals can exploit with their courtship displays. For example, a certain species of bird may eat red berries a lot, so evolves eyes with a high sensitivity to red color, and brains that are attracted by red. This perceptual bias may affect mate choice, predisposing the birds to mate with others who have red rather than blue or yellow plumage. The result would be that the red-biased eyes result in red-biased evolution of courtship plumage (Endler, 1991, 1992). So, many sexually-selected aesthetic displays may originate as side-effects of perceptual adaptations evolved for other functions.

There are some examples of these perceptual biases affecting mate choice. Burley (1988) found that female zebra finches have latent aesthetic preferences for the red and black plastic leg-bands that she used to tag certain males, and not for the yellow or blue bands she put on other males. Of course, male zebra finches of the future will not evolve plastic bands on their legs, but they may very well evolve red coloration, if the right mutations pop up (consider the blue-footed booby of the Galapagos, for example). Basolo (1990) found that female platyfish have latent aesthetic preferences for long plastic "swords" that he glued onto male platyfish tails; in the platyfish's close relatives, the swordtails, those latent preferences seem to have already resulting in males evolving the display. Ridley (1981) argued that the popularity of eye-spots in courtship displays (as in peacocks and argus pheasants) results from animals' general sensitivity to eye-like stimuli. Thus, almost any perceptual bias that animals have can shape how sexual selection plays out, and which courtship displays evolve in a species.

Biologists have documented the importance of perceptual biases in sexual selection for many species (Ryan, 1990; Endler, 1992; Guilford & Dawkins, 1991). Ryan and Keddy-Hector (1992) found that these biases are not randomly distributed, but are typically pointed in one direction. With respect to visual traits for example, all species they investigated preferred bright colors over duller colors, larger displays over smaller displays, and higher contrast over lower contrast. With respect to acoustic traits, all species they investigated preferred calls that were louder rather than softer, more frequent rather than less frequent, longer in duration rather than shorter, lower in pitch rather than higher, higher in complexity rather than lower, and with larger repertoire sizes over smaller repertoires. The relevance to sexual selection for music is obvious: any acoustic preferences that our ancestors had could have been exploited, attracted, and entertained by production of the appropriate musical display.

Aesthetic traits tend to be hard to distinguish from indicators, because in almost all cases, perceptual biases push sexual selection in the same direction that mate choice for reliable indicators would. Lower pitched calls for example are reliable indicators of

body size, because very small animals cannot physically produce very low pitches. Often, traits may function as both aesthetic displays and as indicators (Miller, in press). The power and focus of the two explanations is rather different, however. The advantage of the aesthetic display theory is that it makes us recognize that any aspect of music that we find appealing, could also have been appealing to our ancestors, and if it was, that appeal would have set up sexual-selection pressures in favor of musical productions that fulfilled those preferences.

An important twist on the aesthetic display theory is Fisher's (1930) theory of runaway sexual selection. Fisher considered situations where mate preferences are heritable and courtship traits are heritable, and asked what would happen to both over evolutionary time. He observed that if peahens varied in the length of tail they prefer, and if peacocks varied in their tail lengths, then they would end up mating assortatively, with the length-obsessed females mating most often with the longest-tailed males. Their offspring would tend to inherit both the genes for the long-tail preference, and the genes for long tails, at above-average frequencies. If there was an initial bias in the population, with more females preferring long tails than short, and with more females wanting long tails than there are long tails available, then this assortative mating effect would set up a positive-feedback loop between the mate preference and the courtship trait, leading to ever-more-extreme preferences and ever-more-exaggerated traits. Only when the courtship trait's survival costs became very high might the runaway effect reach an asymptote. Though Fisher's startling idea was rejected for fifty years, it has recently been vindicated by mathematical models (Kirkpatrick, 1982; Pomiankowski et al., 1991).

The power of the runaway theory is that it can explain the extremity of sexual selection's outcomes: how species get caught up in an endless arms race between unfulfillable sexual demands and irresistible sexual displays. Most relevant for us, the preferences involved need not be cold-blooded assessments of a mate's virtues, but can be deep emotions or lofty cognitions. Any psychological mechanism used in mate choice is vulnerable to this runaway effect, which makes not only the displays that it favors more extreme, but makes the emotions and cognitions themselves more compelling. Against the claim that evolution could never explain music's power to emotionally move and spiritually inspire, the runaway theory says: any emotional or spiritual preferences that influence mate choice, no matter how extreme or subjectively overwhelming, are possible outcomes of sexual selection (cf. Dissanayake, 1992). If music that emotionally moves or spiritually inspires tended to sexually attract as well, over ancestral time, then sexual selection can explain music's appeal at every level.

Indeed, sexual selection during human evolution seems to have led to a division of labor between two major courtship displays, with language displays playing upon receivers' conceptual systems, and music playing upon receivers' emotional systems. As a tool for activating specific conceptual thoughts in other people's heads, music is very bad and language is very good. As a tool for activating certain emotional states, however, music is very much better than language. Combining the two in lyrical music such as love songs is best of all as a courtship display.

Music shows many features that can be interpreted as aesthetic displays that fulfil pre-existing perceptual and cognitive preferences. Rhythmic signals are known to be capable of optimally exciting certain kinds of recurrent neural networks as found in mammalian brains. Tonal systems, pitch transitions, and chords probably play upon the physical responsiveness of auditory systems to certain frequency relationships. Musical

novelty attracts attention by violating expectations, overcoming habituation and boredom, and increasing memorability. Music with lyrics reaches deep into cognition through the media of language and imagination.

As with indicators, biology has developed some empirical methods for demonstrating aesthetic displays that could be extended to human music. The first step is to use perceptual experiments to explore the preferences of receivers for various types of stimuli, charting out which kind of stimuli are optimally exciting and attractive. For example, vary the beats per minute of a musical stimulus and see which rhythmic speeds best excite various different feelings in people. The second step is to measure the stimuli actually produced by conspecifics, to see how close they come to being optimally exciting given these preferences. For example, measure the beats per minute in a large sample of commercially-produced songs, and see whether these speeds match the optimal responsiveness curves of human receivers. Many such experiments are pretty obvious, but they become more interesting if the perceptual experiments are extended across closely related species, to see whether the preference is phylogenetically ancient, or whether it evolved to an extreme form through runaway in one species but not in other closely related species. For example, if humans respond best to dance music played at 120 beats per minute, but chimpanzees and gorillas don't respond differently to different rhythmic speeds, then we would have some evidence for runaway selection affecting rhythmic preferences in the human lineage.

Computer simulations of evolution under sexual selection may also prove useful in showing how aesthetic displays evolve (e.g. Enquist & Arak, 1993). My colleagues Peter Todd and Greg Werner have been extending our previous sexual selection simulations (Miller & Todd, 1995; Todd & Miller, 1993, 1997) to model the evolution of musical complexity and variety under mate choice (Werner & Todd, 1997). In these simulations, we have a population of males that produce acoustic sequences and females that receive these sequences. Both males and females are represented as recurrent neural networks with network architectures, connections, weights, and biases determined by heritable genes. Each simulation run is started with randomly-generated male and female genotypes, and all evolution is simply the outcome of the female networks imposing mate choice on the male networks based on the sequences they produce. The runaway effect is possible because the male and female networks can become genetically correlated through assortative mating. We have found that under such conditions, pure sexual selection can favor ever more complex acoustic sequences, and can maintain considerable diversity in such sequences between individuals and across generations (Todd & Werner, 1997).

Order and chaos: The interplay between ritualization and creativity in human music

Human music shows an unusual combination of order and chaos, with some elements highly ritualized and stereotyped, such as tonality, rhythm, pitch transitions, song structure, and musical styles, and other elements highly variable and innovative, such as specific melodies, improvisation, and lyrical content. Hartshorne (1973, p. 56) has commented "Songs illustrate the aesthetic mean between chaotic irregularity and monotonous regularity".

How could sexual selection favor both in a single display medium? With a better understanding of indicators and aesthetic displays, we are in a position to answer.

Ritualization means the evolutionary modification of movements and structures to improve their function as signals (Krebs & Davies, 1987). Ritualization is a typical outcome of signals and displays being under selection to optimally excite the perceptual systems of receivers. Examples of ritualized animal signals include most courtship displays, food-begging displays, warning signals, threat displays, territorial defense displays, play behavior signals, and social grooming behavior. Ritualization results in four typical features: redundancy (repetition over time and over multiple channels), conspicuousness (high intensity, strong contrast), stereotypy (standardized components and units), and alerting components (loud, highly standardized warnings that a more complex signal will follow). Julian Huxley (1969) has observed that

“The arts involve ritualization or adaptive canalization of the creative imagination ... Creative works of art and literature show ritualization in this extended sense, in being ‘adaptively’ (functionally) organized so as to enhance their aesthetic stimulatory effect and their communicatory function. They differ from all other products of ritualization in each being a unique creation (though they may share a common style, which of course is itself a ritualizing agency)”

Here, Huxley introduces the apparent problem: why do human displays such as music contain so much novelty and creativity if adaptive signals tend to get ritualized? The problem with completely ritualized signals is that they are boring. Brains are prediction machines, built to track what’s happening in the environment by constructing an internal model of it. If the senses indicate that the internal model matched external reality, the sensory information hardly even registers on consciousness. Highly repetitive stimuli are not even noticed after a while. But if the senses detect a mismatch between expectation and reality, attention is activated and consciousness struggles to make sense of the novelty. Although ritualization makes signals recognizable and comprehensible, novelty and unpredictability makes them interesting. Adding some unpredictability to signals is the only way to get the signal past the filters of expectation and into a smart animals’ conscious attention.

Thus, sexual selection can often favor novelty in courtship displays. Darwin (1871) observed that in birds, “mere novelty, or slight changes for the sake of change, have sometimes acted on female birds as a charm, like changes of fashion with us”. Large song repertoires, as seen in some bird species like sedge warblers and nightingales, allow birds to produce the appearance of continuous musical novelty (Catchpole, 1987; Podos et al., 1992; Catchpole & Slater, 1995). Small (1993) has emphasized the importance of neophilia in primate sexual selection: “The only constant interest seen among the general primate population is an interest in novelty and variety. Although the possibility of choosing for good genes, good fathers, or good friends remains an option open to female primates, they seem to prefer the unexpected”. In humans of course, neophilia is so intense that it drives a substantial proportion of the global economy, particularly the television, film, publishing, news, fashion, travel, pornography, scientific research, psychoactive drug, and music industries. It seems likely that our hominid ancestors were highly appreciation of novelty, and that this neophilia spilled over into mate choice, where it favored not so much a diversity of sexual partners, but selection of highly creative partners capable of generating continuous behavioral novelty throughout the long years necessary to collaborate on raising children.

The challenge became to convince sexual prospects that you can keep them entertained over long-term relationships, so they don’t get bored and incur the maladaptive costs of

separation and searching again. The main way hominids evolved to do this was through language, using linguistic courtship displays to entertain each other and to indicate their intelligence and creativity. But music could have functioned as another creativity-indicator, and seems to have been sexually selected as such. As with other indicator hypotheses, this one could be tested by seeing whether capacity for musical improvisation and innovation correlates significantly with intelligence and creativity (according to standard psychological measures).

Music in the Pleistocene

Contemporary readers tend to think of music as something made by a tiny group of professionals, after years of intensive practice, using expensive instruments, recorded on digital media, and broadcast by radio, television, or live amplification. And so it is for most of us, most of the time. These technologies permit the production of musical signals far beyond the reach of our Pleistocene ancestors. Even a modest techno dance group like The Prodigy, with just a single principal musician/composer, tour with many truckloads of sound and video equipment, many kilowatts of amplification, and using an armoury of keyboards, samplers, and sequencers that contain vast computational power. The mockingbird's ability to mimic songs of other species is risible compared with the power of modern digital sampling and sequencing equipment. The result is that modern musicians can produce sound sequences that use any possible timbre, at any possible pitch, at any possible speed, and volumes capable of causing permanent deafness.

Music production during human evolution must have been quite different. We know our ancestors lived primarily as highly mobile hunter-gatherers in Africa, and hunter-gatherers cannot carry much stuff around. Still, we should not underestimate the complexity and diversity of music that could have been created in premodern conditions. The human voice is an astoundingly flexible instrument in its own right. Our vocal chords cannot produce two distinct notes at once like the syrinxes of songbirds, but we can produce a great variety of pitches, volumes, and timbres. In fact, almost any musical sequence that can be perceived by humans can be recreated in recognizable form by the human voice. The singing group The Bobs, for example, have recorded a reasonably arousing version of Led Zeppelin's heavy metal classic "Whole Lotta Love". Unaccompanied human voice is sufficient to produce a vast spectrum of musical styles, such as Gregorian chant, Italian opera, Chinese opera, Tibetan throat singing, Meredith Monk's minimalism, Weimar-era Berlin cabaret songs, Baptist gospel singing, Bulgarian women's chants, Irish folk songs, Islamic calls to prayer, Alpine yodelling, and MTV's "Unplugged" concert series. Recall that the haunting yodels of American country singer Slim Whitman were sufficient, in Tim Burton's film "Mars Attacks", to melt the brains of invading aliens if played at even moderate volume. I leave it as an exercise for the reader to imagine whether it could have melted the heart of an ovulating ancestor.

The addition of percussive instruments to the human voice could have come relatively early in the evolution of musical capacities. We do not know when the first proper drum, with a stretched skin over a resonating chamber, was invented. But, as any parent of an acoustically extroverted toddler knows, it is not difficult for a determined percussionist to improvise given ordinary objects. Strike two rocks together once, and you have noise. Strike them together twice, and you have rhythm. Rocks are not the best natural material though. Wood, bamboo, and bone are better. Bones are especially convenient, because they are natural by-products of hunting, and are often hollow. Human skulls for

example, are often used to make the Tibetan ritual drum called a damaru. Many other materials work to make simple rattles, stampers, clappers, and scrapers. The San people of southern Africa make ankle rattles out of springbok ears sewn together and filled with pebbles. Clamshells can be clapped together with two hands. A scraper can be made by rasping the jawbone of a bison with its femur. The top of a gourd can be broken off and the open end pounded against the ground, as in Western Africa, or in and out of water, as in the Solomon Islands, or beaten with sticks. More complex are the slit gongs of Africa, where a log is hollowed out, carved with slits, and beaten to produce up to seven different tones.

In terms first developed by musicologist Curt Sachs in the 1930s, these are all “idiophones”, which make sounds from their own material, as opposed to membranophones (with a stretched skin, such as a drum), aerophones (with a tube to blow through, like a trumpet), or chordophones (with a stretched string, like a violin). Idiophones may well have been used hundreds of thousands of years ago, while the other three types were very probably invented more recently, in the last hundred thousand years. All cultures have idiophones, but not all have the other types. Australian aborigines, for example, did not have drums (membranophones), only clapsticks (idiophones) and drone pipes (aerophones). Even if restricted to idiophones, a very wide range of rhythmic patterns are possible, especially in groups with different people playing different rhythm lines (see Arom, 1991).

The recent discovery of a Neanderthal bone flute of 40,000 years ago suggests not only that aerophones are reasonably ancient, but also that Neanderthals made music, and that, based on acoustic analysis of the flute’s hole spacing, they preferred the same pentatonic scale that pervades human folk music. Many Upper Paleolithic cave paintings of the same era portray dancing and the use of idiophones. Together with the universality of singing, rhythmic drumming, and dancing across all human cultures (some of which, like the Australian aborigines, have been genetically distinct for at least 40,000 years ago), this evidence suggests that human music was both common and sophisticated by 40,000 years ago. The ease of making idiophones out of readily available Pleistocene materials would also give scope for percussion instruments to be something on the order of a million years old. Despite the lack of Zildjian cymbals, Stratocaster guitars, and Fairlight synthesizers, there would have been plenty of opportunity for our ancestors to make decent music a very long time ago.

Nor should we confuse the production of musical signals permitted only by modern technology with the production of musical experiences. Contemporary rock concerts are much louder, and use a wider variety of timbres than ancestral music could have, but an evening of rhythmic dance in tribal societies seems to produce effects at least as intense. Traditional music in tribal societies has a few key features that distinguish it from music as we tend to enjoy it in modern society, and that are much more likely to represent the music made by our ancestors. First, music is almost always a group affair, with everyone actively participating and no one simply sitting and listening contemplatively. Competence at music and dance was probably expected of every sexually mature adult, instead of being the speciality of a few schooled professionals. Second, music is almost always accompanied by dancing, such that to enjoy music and to dance to it are virtually synonymous. There were probably no Pleistocene “concerts” with hundreds of hominids sitting in rows for hours, meditatively listening without moving a muscle, like bourgeois symphony-goers. The young Londoner dancing all night at a rave makes a much accurate model for how our ancestors appreciated their music.

Third, ancestral groups were small, egalitarian, and informal, so none of music's functions in military marches, state coronations, national anthems, or other rituals of our vast, hierarchical societies would have been relevant to music's evolutionary origins.

Why is human music so different from acoustic courtship in other species?

This question is a special case of the general quandary: why are humans so unique, with extra-large brains, intelligence, culture, and creativity? There are three basic answers available from evolutionary theory: (1) humans had different phylogenetic origins from other species, arising from anthropoid apes, (2) human ancestors faced different selection pressures in their ancestral environment, reflecting the demands of the African savanna habitat, the hunter-gatherer econiche, group-living, etc., (3) the random effects of mutation and genetic drift, interacting with positive-feedback processes that amplify these stochastic effects. All of these are important, but I think the interaction of group-living and runaway sexual selection provide the key. Music is what happens when a smart, group-living, anthropoid ape stumbles into the evolutionary wonderland of runaway sexual selection for complex acoustic displays.

But ideally, we need more specific hypotheses linking specific features of the ancestral environment to specific features of music. One feature of music is that its attractions work indirectly rather than immediately. This is a luxury allowed by living in stable social groups. Primates are highly social, and anthropoid apes have particularly high social intelligence and complex social strategies (Whiten & Byrne, 1997). Our hominid ancestors almost certainly lived in large groups where they developed complex, long-term relationships with many relatives and non-relatives. There would have been lots of time to develop in-depth assessments of which non-relatives might make good mates. Rather than relying on short-term courtship displays as so many non-social species do, hominid courtship could have been a subtle, low-key, long-term affair. Courtship displays did not have to provoke immediate copulation; they only had to insinuate themselves into the memory of a sexual prospect, influencing their mating decisions in the months and years to come.

Another feature of music is how exhausting its performance tends to be in hunter-gatherer tribal societies. People dance a long time, and get really tired in doing so. Many anthropologists have observed that human hunting strategies are rather different from those of other carnivorous animals, relying on projectile weapons to injure prey, which are then chased for hours until they drop from injury and exhaustion. This type of "persistence hunting", which relies on the long-range running, high aerobic capacity, and sweating ability of humans, creates incentives for mate choice to focus on indicators of ability to maintain good motor control under conditions of high aerobic effort over long periods. Because most courtship happens in the evening when the sexes are in the same place, and because it would be impractical for females and males to run around after each other in the dark to see how far they can go, our hominid ancestors evolved the convention of dancing around in place, with everyone in the group using the same rhythm. Most tribal and folk dancing includes repeated high stepping, stamping, and jumping, using the largest, most energy-hungry muscles in the human body. One could not ask for a better test of aerobic endurance (before modern sports medicine treadmills) than the coordinated group dancing of human tribal societies. Many anthropologists tend to report that tribal dancing involves all members of the group, but I can scarcely believe that the very young, the old, the sick, and the injured, would dance quite as long

or as hard as the young, healthy, and single. We desperately need more quantitative data from cultural anthropologists on such questions.

If sexual selection shaped music, why is music made in groups?

Many theories about the evolution of music suggest that, since traditional tribal music is almost always made in groups where everyone participates and dances, music must have some kind of group-level function rather than an individual-level function such as sexual selection would suggest. Indeed, there is a quandary here, but it is not a serious one.

Some male birds display their charms in large congregations known as “leks”, strutting, displaying, and sometimes singing by the dozens or hundreds (Balmford, 1991). Such congregations make it efficient for females to wander around the lek, searching for good males. The apparent “group display” in such species apparently results from natural selection to minimize search costs for females, pushing males to congregate and compete in local clusters. Likewise, many male frogs and insects produce their songs in the same area, resulting in large “choruses”. Sometimes, these males take turns singing so females have some hope of locating at least one of them. Thus, apparently coordinated group displays can sometimes arise through the interaction of selfishly displaying males, without any group selection.

It is crucial to distinguish between behaviors done in groups and behaviors done for groups. Primates are highly social, often group-living animals. Although almost all of their daily behavior is groupish, with intense, intricate, dynamic social interactions, primatologists have never found it necessary to invoke group selection to explain any primate behaviors. Quite the opposite: progress in primatological studies of social behavior boomed after the ‘selfish gene’ revolution in biological theory, which showed why group selection almost never works (Williams, 1966; Wilson, 1975; Dawkins, 1976). Unfortunately, this sort of methodological individualism, which views group-level effects as emergent phenomena arising from selfish interactions between individuals, has never become very popular in cultural anthropology or musicology. This has created a persistent problem: the fact that music is made in groups is almost always interpreted as meaning that the music is made for groups, and that this putative group-level function is most important both biologically and culturally.

The trouble with music evolution theories that invoke group-level functions is that they usually end up explaining music through group selection, explicitly or implicitly. For example, group production of music is said to result in a “group-bonding” effect, which supposedly facilitates group cooperation and mutual understanding (Freeman, 1996; Richman, 1987), which in turn supposedly gives the group an advantage over other groups with less effective group musical behavior. Other theorists view music as a means for a group to remember and perpetuate its shared values and knowledge (e.g. Farnsworth, 1969; Nettle, 1983; Sloboda, 1985), or for a group to coordinate rhythmic work (which, unfortunately for the theory, is almost absent among hunter-gatherers). Even sociobiologist E. O. Wilson (1975) fell into positing a group function for music.

There is nothing illogical or impossible about group selection models as theoretical possibilities (see Boyd & Richerson, 1990; Miller, 1994; Wilson, 1997; Wilson & Sober, 1994;). However, there are two errors theorists commonly make when invoking group

selection in specific situations. The first error is ideological: group selection is often favored because it is thought to be a kinder, gentler, more cooperative, more humane form of evolution than individual level selection, more suited to the production of positive, enjoyable adaptations like language, art, and music. But group selection, like all selection, depends on competition, with some groups winning and some groups losing. Biologist George Williams has observed that group competition replaces the logic of murder with the logic of genocide. Not a great moral improvement. Group selection models of music evolution are not just stories of warm, cuddly bonding within a group; they must also be stories of those warm, cuddly groups out-competing and exterminating other groups that don't spend so much time dancing around their campfires.

The second common error about group selection is failing to consider free-riding: ways that individuals could enjoy the group benefits without paying the individual costs. If this is possible, then selfish mutants can invade the cooperating groups, eroding the power of group selection and the utility of the group-selected adaptation. Suppose an ancestral group evolves a "Rave" gene that makes them dance every night, doing their group-bonding thing, enjoying their group-competitive advantages over other less musical groups. Then, perhaps a "Wallflower" mutation emerges among these People of the Rave, which predisposes its possessors to rest while their comrades dance. Because the wallflower mutant does not pay the enormous time and energy costs of dancing all night, but still enjoys the advantages its group has over other groups, the Wallflower mutant inevitably spreads through the People of the Rave. Within a few generations, the music would go away, and we would be back to a population of well-rested wallflowers. If there is no individual-level advantage to musical behavior, and there are individual costs, then group selection would have great difficulty having any effect on the evolution of music. The same holds true for any other "altruistic" trait that has individual costs and only group benefits. No biologist has ever made a good case for such an altruistic trait ever having evolved in any vertebrate species, so it is not the kind of explanation one would wish to invoke for human music. (It should go without saying that anthropological claims that some tribes have "no concept of the separate individual" have no bearing whatsoever on the scientific status of group selection versus selfish-gene theory in human evolution. Animals do not need to know they're individuals for selection to act on them as such.)

On the other hand, we mustn't be dogmatic about group selection always being an unworkable or outdated idea. If music did have individual-level benefits, such as courtship benefits under sexual selection, then it may be possible for group selection to reinforce those individual benefits with group benefits. Under this model of group selection, there would be no necessary tension between the individual and group levels of selection: music would not be "altruistic", with individual costs and only group benefits. If none of the Ravers were willing to mate with a Wallflower, the Wallflower gene could never invade the group. This type of group selection model has been very poorly studied in theoretical biology, but it is not implausible (see Boyd & Richerson, 1990). I think this sort of interplay between sexual selection and group selection may be the only sensible way to introduce group selection into models of music evolution.

Another overlooked factor is kin selection, which is easy to mistake for group selection when groups are composed largely of genetic relatives. However, to posit that music evolved under kin selection, for some kind of kin-bonding function, seems implausible, because no other species with cooperation between kin requires any special bonding

ritual. Nor does music and dance seem to play the major role in family groups that it plays when non-kin come together.

The main appeal of the group-bonding argument is, I think, our subjective experience that music feels better when there are others around enjoying it too. The production of this warm groupish glow, delight, or euphoria should not be mistaken for music's adaptive function, however. If music evolved principally under sexual selection, it would make sense for music enjoyment to be greater when one is surrounded by a large number of others, especially young, attractive, single others. Rock concerts make teenagers feel giddy with excitement not because they will feel an oceanic oneness with their peers in any behaviorally significant way -- there are too many fights after concerts for that theory to work -- but because concerts afford an excellent opportunity for meeting partners. It is not necessary for us to be aware of this adaptive logic for it to have worked over many millenia in shaping the group production and enjoyment of music. Apart from mating, the experience of producing music in a large group may feel good simply for mood-calibration purposes (see Tooby & Cosmides, 1990). Singing lyrical music together, for example, would have given powerful evidence under ancestral conditions that one was part of a successful band: a large group of healthy, energetic people with few social tensions who share a common language.

Many ethnomusicologists (e.g. Nettl, 1983) take a different view on music's group-bonding functions, and seem at certain points to view music as a means for collective access to the supernatural. This merits a brief evolutionary critique: accessing the supernatural can only be the adaptive function of a biological trait such as music if the supernatural actually exists, and if accessing it gives concrete fitness benefits. Evolution would not be impressed by animals that merely *think* they attain god-like powers through music; they would *really have to do it* for selection to favor this function. Of course, convincing others that there is a supernatural, and that one has special powers to access it, might function as a perfectly good courtship display. Composers who view music as an intermediary between humans and gods (e.g. Stravinsky, 1947) are, of course, setting themselves up for worship as high priests, without taking any vows of celibacy.

A plea for more quantitative behavioral data on music production and reception

As we have seen, evolutionary biology has a rich set of theories concerning sexual selection and animal signal systems, and an ever more sophisticated set of behavioral research methods for testing hypotheses about the functions of animal signal systems such as human music. However, these methods demand much more detailed quantitative data about music production and reception than are typically available from ethnomusicology, psychomusicology, or cultural anthropology. In terms of quantitative data relevant to sexual selection hypotheses, we know more about the calls of the small, drab, neotropical Tungara frog *Physalaemus pustulosus* (Ryan, 1985), than we do about human music.

There are some key questions that need further research. To test the hypothesis that music production functions in part as a set of sexually-selected indicators, we need to know much more about: (1) the genetic heritability of musical capacities in modern human populations, (2) the genetic heritability of relevant fitness components such as displays might indicate, such as intelligence, creativity, aerobic capacity, and motor

control, (3) the phenotypic correlations between musical capacities and the underlying traits they represent, (4) the mate preferences people have concerning musical displays, and the inferences they make from manifest musical ability to underlying traits, and (5) the sexual payoffs for different degrees of musicality in tribal and modern populations. To test the hypothesis that music production functions in part as a set of aesthetic displays, we need to know much more about (1) the perceptual and cognitive preferences people (and other apes) have with respect to many dimensions of musical stimuli, (2) the frequency distribution of actual musical productions with respect to those dimensions, (3) whether there is strong assortative mating for musical traits, and (4) whether there are genetic correlations between musical tastes and music-production tendencies in modern populations, which might indicate a runaway effect in progress.

To test the more general hypothesis that sexual selection through mate choice has been a major factor in the evolution of human music, we need to see whether music production behavior matches what we would expect for a courtship display. There is some suggestive evidence in this direction. I took random samples of over 1800 jazz albums from Carr, Fairweather, and Priestley (1988), over 1500 rock albums from Strong (1991), and over 3800 classical music works from Sadie (1993), and analyzed the age and sex of principal music-producer for each. The resulting plots indicated that, for each genre, males produced about 10 times as much music as females, and their musical output peaked in young adulthood, around age 30, near the time of peak mating effort and peak mating activity. This is almost identical to the age and sex profiles discovered by Daly and Wilson (1988) for homicides, which they took as evidence for sexual selection shaping propensities for violence sexual competitiveness. Here, the same profiles suggest that music evolved and continues to function as a courtship display, mostly broadcast by young males to attract females. Of course, my samples may be biased, because only the best musicians have opportunities to record albums or have their works documented in classical music encyclopedias. However, Simonton's (1993) studies of creativity suggest that the demographics of extremely creative cultural production are not significantly different from the demographics of ordinary cultural production, so the former can usually be taken as a proxy for the latter. If so, it seems likely that most music at all levels, from local pub bands to internationally televised concerts, is produced by young men. And that is the exactly the pattern sexual selection would produce (see Buss & Schmitt, 1993; Daly & Wilson, 1994).

In any case, for evolutionary studies of human music to flourish, we need to adopt the same quantitative methods that have worked so well for studies of signalling systems in other species (Hauser, 1996; Martindale, 1990; Simonton, 1991, 1993). Music must be viewed as a behavior generated by signallers and sent to receivers, rather than as an abstract system of communication, emotion, and cultural meaning. The behavioral details of music production and reception are much more informative about music's evolutionary origins and adaptive functions than the details of music as a disembodied formal system. Studies of language evolution provide a cautionary tale in this respect: two hundred years of speculation about the origins of human language have shed virtually no light on language's survival and reproductive payoffs, because language has usually been treated as an abstract system of syntax, morphology, and vocabulary (e.g. Bickerton, 1995; Pinker, 1994), rather than a concrete behavior with some people talking to others in ways that affect their fitness.

Conclusion

“Although ornithologists and acousticians agree about the musicality of the sounds uttered by birds, the gratuitous and unverifiable hypothesis of the existence of a genetic relation between bird song and music is hardly worth discussing” Levi-Strauss (1970, p. 19)

Cultural theorists such as Levi-Strauss have been too quick to dismiss evolutionary analogs of human music. Bird song and human music do not share a common phylogenetic origin, but they may very well share a common adaptive function. This chapter has argued that the functional analogs between human music and animal acoustic courtship have been dismissed too readily, too contemptuously, and with too little appreciation of sexual selection theory.

Sexual selection through mate choice is almost unfairly powerful as an evolutionary explanation for things like music that seem impressive and attractive to us, but that seem useless for survival under ancestral conditions. The reason is that any feature you're even capable of noticing about somebody else (including the most subtle details of their musical genius) is a feature that could have been sexually selected by our ancestors. If you can perceive the quality, creativity, virtuosity, emotional depth, and spiritual vision of somebody's music, then sexual selection through mate choice can notice it too, because the perceptions of ancestors with minds like yours were literally the agents through which sexual selection operated. If both musical tastes and musical capacities were genetically heritable (as practically all behavioral traits are -- see Plomin et al., 1997), then runaway sexual selection would have had no trouble in seizing upon early, primitive, acoustic displays and turning them over thousands of generations into a species-wide adaptation known as music.

This chapter has advanced just a few rather obvious ideas about the evolution of music, first articulated by Darwin, but worth reiterating in the light of contemporary biology. Music is a biological adaptation, universal within our species, distinct from other adaptations, and too complex to have arise except through direct selection for some survival or reproductive benefit. Since there are no plausible survival benefits for music production, reproductive benefits seem worth a look. As Darwin emphasized, most complex, creative acoustic displays in nature are outcomes of sexual selection and function as courtship displays to attract sexual partners. The behavioral demographics of music production are just what we would expect for a sexually-selected trait, with young males greatly over-represented in music-making. Music shows several features that could function as reliable indicators of fitness, health, and intelligence, and as aesthetic displays that excite our perceptual, cognitive, and emotional sensitivities. Opportunities for both music production and selective mate choice would have been plentiful under ancestral hunter-gatherer conditions. In short, the evolutionary analogy between bird song and human music may be much closer than previously believed: both are sexually-selected courtship displays first, and fulfil other functions less directly.

There is plenty left to do. We need much more quantitative behavioral data on music production and reception, of many different types, ranging from genetic heritability studies, to physiological studies on the costs of music-playing and dancing, to perceptual experiments on music preferences. There is still the quandary of why individual courtship displays would be produced in groups, and whether group selection may have interacted with sexual selection in music evolution. There is scope for more computer simulations of how musical complexity and novelty might evolve under sexual selection.

More centrally, the design features of human music need to be related much more securely and less speculatively to specific functions under ancestral conditions.

Progress concerning music evolution seems most likely by adopting the same adaptationist approach that has proven so fruitful in understanding bird song and other complex signal systems. Modern biology provides a great wealth of evolutionary theory and empirical methods, many of which can be applied with little modification to analyzing human music. To many musicologists, this may seem a radical approach, threatening a psychologically and genetically reductionist view of music. To students of sexual selection, however, to say that a human adaptation has been shaped by mate choice is grant it the least reductionistic, most humane origin, as a part of the mind selected by minds like ours for its ability to provide mental and emotional enjoyment. Music arose as a natural outcome of psychology mixing with sexuality in the genetic stream that became humanity.

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